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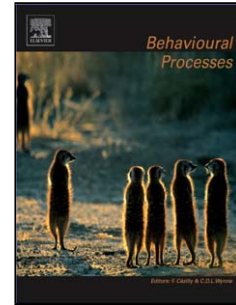
Title: Infanticide risk and infant defence in multi-male free-ranging Sooty Mangabeys, *Cercocebus atys*

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1 **Infanticide risk and infant defence in multi-male free-ranging Sooty Mangabeys, *Cercocebus***
2 ***atys***

3

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5

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10

11 **Abstract**

12 For years, infanticide by males was thought to be unlikely in multi-male primate species. Recent
13 studies have, however, presented evidence of infanticide in such species and a recent model by
14 Broom and colleagues predicts that males' age and rank influence the occurrence of infanticide:
15 youngest and highest ranking immigrant males are more likely to commit infanticide than their
16 older and lower ranking counterparts if putative fathers fail to protect infants. I collected data on
17 adult free-ranging sooty mangabey females in the Taï National Park, Ivory Coast, over eleven
18 months including a birth and a mating season. Infanticide had been previously reported in captivity
19 for this species, but not in the wild. Several males entered the group prior to and during the mating
20 season. As predicted by the model, only the more dominant immigrant ones attacked mother-infant
21 pairs significantly more often than did other males. Mothers often reacted with counter-attacks.
22 Potential fathers guarded and supported infants and mothers throughout the period of infant
23 vulnerability. Furthermore, as only one of seven infants died despite 136 observed attacks on
24 mother-infant pairs and unattended infants by immigrant males, we conclude that cooperation
25 between putative fathers and mothers represents an effective protection against infanticide.

26 (199 words)

27

28 Keywords: cooperation; counter-attacks; model; resident and immigrant male

29

30 INTRODUCTION

31 Deliberate killing of infants by adult males has been reported for many mammal species and
32 is frequent in primates (e.g. Hrdy 1974, Angst & Thommen 1977, Janson & van Schaik 2000, van
33 Schaik 2000). No less than five explanations have been proposed, including, among others, the
34 social pathology hypothesis (Dolhinov 1977, Boggess 1984) that predicts infanticide in primates
35 living in unnatural environments and the by-product hypothesis (e.g. Sussman et al. 1995) in which
36 infanticide is a side effect of males' general aggression. The most widely accepted explanation for
37 infanticide in non-human primates however, is the sexually selected infanticide hypothesis (Hrdy
38 1974, 1979, Hrdy & Hausfater 1984). It states that an adult male may increase his fitness by killing
39 unrelated and unweaned infants if he can easily mate with the mother afterwards: the female victim
40 of infanticide immediately resumes her sexual cycle and after having defeated the former resident
41 male, the infanticidal male gain an earlier opportunity for siring the next offspring (e.g. Borries et
42 al. 1999a, Pussey & Packer 1994, contributions in van Schaik & Janson 2000). Hence, in its
43 original formulation, this adaptive scenario was restricting infanticide to non-seasonal breeders
44 characterised by a single-male mating system. However, many studies reported infant killing by
45 males in both multi-male (e.g. Collins et al. 1984, Borries et al. 1999a, Soltis et al. 2000, Weingrill
46 2000) and seasonal breeders (e.g. Wright 1995, Borries 1997) and this new range of infanticide
47 occurrences led to new predictions about the way males may gain reproductive benefits. In multi-
48 male breeders, newcomer males are then expected to use infanticide if they reach a status in the
49 male hierarchy that allows them to mate with females (Broom et al. 2004). In seasonal breeders,
50 males are expected to commit infanticide quite early after the infant's birth so that females can

51 resume ovulation either before the end of the mating season or right at the very beginning of the
52 next one (see Wright 1995).

53 In species in which males tend to commit infanticide, females are expected to develop
54 counter-strategies to minimize the risk of infant loss (Hrdy 1979; Smuts & Smuts 1993). A first
55 strategy involves behavioural changes during the period after birth when infants are vulnerable to
56 infanticide. This can include avoiding unfamiliar males or constraining infants in their presence
57 (e.g. Collins et al. 1984, Fairbanks & Mc Guire 1987, Hauser 1988, Sommer 1994, Wright 1995),
58 counter-attacking infanticidal males (e.g. Mohnot 1971, Hrdy 1977), and finding allies such as
59 related females or potential fathers to help them protect infants (e.g. Smuts & Smuts 1993, Treves
60 1998, 2000, Borries et al. 1999b, Palombit et al. 2000). A second strategy involves behavioural and
61 physiological changes prior to conception. Since most male primates are thought to be unable to
62 recognise their offspring as such (e.g. König 1989, but see Alberts 1999, Buchan et al. 2003), they
63 probably restrain their aggressive behaviours towards infants of females they mated with (Noë &
64 Sluifster 1990, van Schaik & Kappeler 1997). Thus, females can mate promiscuously in order to
65 induce paternity confusion (Hrdy 1979, Hrdy & Whitten 1987, Nunn 1999, van Schaik et al. 1999)
66 or display sexual swellings at times it is unlikely for them to be ovulating (Gordon et al. 1991,
67 Zinner & Deschner 2000). In this paper we only focus on the first option, i.e. behavioural changes
68 during infant vulnerability.

69 Mangabeys (*Cercocebus spp.*) are both promiscuous and seasonal breeders and infanticide
70 occurrences have been reported in both captive sooty mangabeys (*C. torquatus atys*, Busse &
71 Gordon 1983, Gust et al. 1995) and free ranging crested mangabeys (*C. galeritus galeritus*, Gust
72 1994). Preliminary observations of several non-resident males attacking mothers and infants in our
73 study group gave us reason to suspect infanticide to occur in wild sooty mangabeys (*C. torquatus*
74 *atys*) as well. In our group the average inter-birth interval was 29 ± 7 months (N = 28 females) and
75 females who lost their infants during the six-months period after birth immediately resumed

76 menstrual cycles while females whose infants remained alive or lived longer than six months did
77 not. Thus, non-resident males could gain an earlier opportunity to mate with mothers (at least a
78 whole year) by committing infanticide at an early stage after infants' births. We therefore
79 investigated the potential risks for infanticide and their likely consequences. We first hypothesised
80 that if infanticide may occur, it would essentially be performed by non-resident males. Hence, we
81 expected (1) these males to mainly target mothers and infants rather than other members of the
82 group. More precisely and as suggested by the recent model from Broom and colleagues (2004), we
83 expected (2) these aggressive males to be young and to sufficiently integrate the group to quickly
84 rise in the male hierarchy. Secondly we hypothesised that if infanticide risks were real, some adult
85 members of the group would develop counter-strategies. More particularly, we expected (3)
86 potential fathers to actively protect mothers and infants and (4) females to seek the proximity of
87 these males. Eventually and still following the model by Broom and colleagues (2004), we
88 expected (5) these protector males to be older and dominant resident males.

90 METHODS

91 **Research area and subjects**

92 This study was conducted in the Taï National Park in south-western Ivory Coast (6°20'N to
93 5°10'N and 4°20'W to 6°50'W). The park is the last remaining major block of West Africa primary
94 forest. It covers approximately 454,000 ha. With a mean annual rainfall of 1875 mm, a mean
95 annual temperature of 24°C (Taï Monkey Project data, 1991-1999) and a distinct dry season from
96 December to March, the forest is classified as “tropical moist forest” (Whitmore 1990). At least
97 twelve primate species, including sooty mangabeys (*Cercocebus atys*), live in the park.

98 The group was well habituated to human observers prior to the start of this study and was
99 followed from dawn to dusk by at least one observer during the entire study period from November
100 2001 to August 2002. During this period, 7-14 adult males, 35 adult females, about 70 sub-adults

101 and juveniles were observed in the group. Seven infants were born between December 10, 2001
102 and March 10, 2002. Seven of the adult males (“residents”) were present in the group over the
103 entire study period. Altogether, seven other adult males (“non-residents”) joined the group for
104 various periods of time during this period. Five of those (“immigrants” males) entered the group in
105 February, stayed until the end of the study and integrated the male hierarchy. The two other non-
106 resident males remained in the group for very short periods (from a couple of hours to a couple of
107 days at a time). We therefore focused the analyses on the five immigrant males only.

108 On average, mangabeys (*Cercocebus spp.*) have a gestation period of about six months
109 (Deputte 1991) and a lactation that can vary between four/five months (wild *Cercocebus albigena*
110 *johnstonii*: Rowell & Chalmers 1970) and six/ten months (*C. galeritus* in Groves 1978). In our
111 study species (*C. torquatus atys*) the lactation period seemed to last longer (from 12 up to 18
112 months). However, this difference may result from the fact that no accurate terminology defines
113 when a lactation period really ends. In our group, the six surviving infants of the year started to eat
114 diverse food around five/six months but were still suckling regularly. At least 21 juveniles born the
115 previous years were still regularly suckling at the beginning of the study: 13 of them stopped when
116 they were about 12 months old and the rest carried on to regularly suckle and cling on mothers till
117 after they were 18 months old. The birth season was comprised between December and March with
118 a peak around February (Range & Noë 2002). The mating season usually started in May and lasted
119 up to the end of September with a mating activity peak in July-August.

120

121 **Data collection**

122 The analyses presented in this paper are based on conflicts and proximity data recorded
123 during focal animal and *ad libitum* sampling (Altmann 1974). Conflicts were recorded when one
124 individual threatened, darted at and potentially chased over few meters, pushed on the ground or bit
125 another individual. Proximity was considered when two individuals were less than 5 meters apart.

126 We conducted 15-min focal samples on adult females with at least 60 minutes between
127 consecutive samples of the same individual and three minutes between samples of different
128 individuals. However, for the analyses we also used the focal samples that were at least nine
129 minutes long (89 samples over 2272) if they were truncated because of the observer losing the
130 subject after an obstacle. For each focal animal, we recorded each minute on the minute
131 (instantaneous sampling, Altmann 1974): the infant's presence / absence and distance and the
132 nearest adult female and male within 5 meters. Social interactions were recorded continuously
133 (detailed ethogram in Range & Noë 2002). Due to limited visibility in the early evening, we opted
134 for an opportunistic sampling schedule conducting focal samples only between 7 a.m. and 4 p.m.

135 Between November 1, 2001 and August 20, 2002 we collected 1360 hours worth of *ad*
136 *libitum* data and a total of 568 hours of focal samples for all of the 35 adult females (ranging from
137 63 to 65 per female).

138

139 **Data Analysis and statistics**

140 Each time we performed analyses between categories of individuals, we corrected for their
141 respective numbers: resident males: $N = 7$, immigrant males: $N = 5$, mothers: $N = 7$, non-mothers:
142 $N = 28$, juveniles between one and two years old: $N = 21$ and unattended infants: $N = 6$.

143

144 Dominance

145 We compiled two socio-matrices (one for adult males, one for adult females) in which we
146 used the recorded approach/retreat and threat/retreat unidirectional interactions to determine the
147 subordinate individual of each dyad. For both males and females, the rank-order among adults was
148 strictly linear (Matman with 10000 randomisations: Kendall's coefficient of linearity: $K = 0.967$ for
149 both gender, $\chi^2 = 48$, $p = 0.0017$, $df = 25.12$ for males, $\chi^2 = 447.89$, $p < 0.0001$, $df = 40.86$ for
150 females).

151

152 Infants' vulnerable period to infanticide

153 As females whose infants died within the six months after birth were observed to resume
154 menstrual cycles, we assumed these six months to be a good estimate of the period during which
155 males would benefit more from infanticide. Hence, we defined these six months as the period
156 during which infants may be vulnerable to infanticide (vulnerable period VP hereafter).

157 During the vulnerable period, infants grew more and more independent and could be left
158 unattended for short periods of time. We defined infants as being unattended when they were at
159 more than three meters from their mothers for more than one minute. One infant died while he was
160 still continuously clinging on his mother so we removed him from analyses performed on
161 unattended infants.

162

163 Statistics

164 Non-parametric statistical tests (Siegel & Castellan 1988) were conducted using Statview
165 (version 5.0.1). Analyses of conflicts and male-female proximities were conducted using Chi-
166 square (χ^2), Mann-Whitney-U tests and Spearman correlations. Results were considered as being
167 significant when $p \leq 0.05$. If multiple n tests were conducted on the same data set, we set the total
168 experiment wise error rate α at 0.05 and the corrected α' were taken from Narum reference table
169 with critical values for the Bonferroni correction method (2006).

170

171 RESULTS

172 **Pattern of aggression of adult males towards females and infants**

173 In order to test the hypothesis of infanticidal risk, we analysed the pattern of aggression of
174 adult males toward adult females, juveniles and unattended infants. During the study, we observed
175 154 conflicts between adult males and adult females, 117 of which were conducted by immigrant

176 males (attacks against mothers: $N = 92$, attacks against non-mothers: $N = 25$) and 37 by resident
177 males (mothers: $N = 8$, non-mothers: $N = 29$). Immigrant males were significantly more aggressive
178 towards mothers than towards non-mothers (two-tailed Chi-square test $\chi^2 = 81.408$, $p < 0.001$, $df =$
179 10). Resident males, in contrast, attacked mothers at similar rates than they attacked non-mothers
180 (two-tailed Chi-square test $\chi^2 = 0.084$, $p = 0.999$, $df = 1$) (Fig. 1). On average, over the whole 1360
181 hours we spent observing the study group, an immigrant male would be likely to attack a female
182 with infant 2.63 times while he would only attack a female without infant 0.18 times.

183 The attacks from both male categories were very distinct. Attacks from immigrant males
184 started as soon as they entered the study group. Usually they would dart at mothers, coming quickly
185 on their back and would grab their fur or a part of their infant's body, push them on the ground and
186 quickly try to bite. Females would loudly scream and look around for support. In contrast, resident
187 males mainly tended to slap females during the reproductive season. Usually a female at the
188 beginning of her menstrual cycle would start to present her sexual parts to males. Old resident
189 males would inspect them once or twice before turning around. Then the female would leave.
190 However, some would insist and present again and again leading the male to threaten and slap
191 them.

192
193 Immigrant males conducted 36 attacks against unattended infants and only 2 against
194 juveniles between one and two years of age. In contrast resident males never attacked unattended
195 infants and attacked juveniles four times. Immigrant males significantly targeted unattended infants
196 more than juveniles of less than two years (two-tailed Chi-square test $\chi^2 = 42.318$, $p < 0.0001$, $df =$
197 1). Due to the small sample size for resident males, we did not perform any statistical analysis.

198
199 Among the immigrant males, we found a negative correlation between the rate of
200 aggressive behaviours and their respective rank-order in the group (spearman correlation: $r = -1$, p

201 = 0.0455). As suggested by Broom and colleagues (2004), higher-ranking immigrant males were
202 more aggressive toward mothers and infants than their lower-ranking counterparts. Furthermore,
203 we also found a positive correlation between the number of mounts they could perform and their
204 respective rank-order (spearman correlation: $r = 0.98$, $p = 0.0456$). In fact, two of the immigrant
205 males reached the male alpha position during the mating season. During their tenure, they could
206 form consort and mate with receptive females without being displaced by other adult males.

207 Unfortunately, as immigrant males were coming from non-habituated groups, we could only
208 have a rough estimation of their age. Hence, we did not try to correlate their age with their level of
209 aggression.

210

211 **Pattern of aggression among adult males**

212 In order to test the hypothesis of infant protection by resident males, we analysed conflicts
213 among adult males. We observed 178 conflicts among the five immigrant and seven resident adult
214 males. Immigrant males attacked another adult male (resident or immigrant) 20 times while
215 resident males attacked 158 times. A resident male was significantly more likely than an immigrant
216 male to attack another adult male (two-tailed Chi-square test $\chi^2 = 38.398$, $p < 0.0001$, $df = 1$).
217 Among these resident males, two males showed significantly higher rates of aggression towards
218 other males (150 attacks; two-tailed Chi-square test $\chi^2 = 90.455$, $p < 0.0001$, $df = 1$ and Chi-square
219 test $\chi^2 = 15.828$, $p < 0.0001$, $df = 1$) (Fig. 2). Of these 150 attacks, 129 (86%) were directed towards
220 immigrant males after they had first attacked mother/infant pairs or unattended infants (Fig. 3).

221 To summarize: immigrant males attacked mother/infant pairs and unattended infants 128
222 times. The two resident males protected females and infants by themselves on 116 occasions and
223 simultaneously on 13 occasions. We henceforth categorised them as “protective” (PR) males. The
224 protection could vary from a simple threat (opened mouth with visible teeth) with a slight forward
225 movement of the body to chases, slaps and bites. The threat mainly happened when females had

226 counter-attacked with other females (five times) or when infants were already more than three
227 months old and clinging on their mothers (47 times). Chases and slaps occurred when a PR male
228 darted at an immigrant male: when this male remained close to the females or infants (20 times),
229 the PR male slapped him on the face and shoulders; when he jumped and fled (44 times), the PR
230 male chased him over long distances (> 50 meters) for few minutes. Eventually, the PR males'
231 simultaneous actions were the most intense. One PR male would first dart at the immigrant male
232 and the second PR male would follow few seconds afterwards. The three males would end up
233 rolling on the ground with many grunt vocalisations and biting each other. All 13 actions occurred
234 after immigrant males tried to grab and bite unattended infants.

235 It is to note that outside the infant context, males hardly fought each other. Indeed we
236 recorded only 49 fights and all occurred during the mating season. One immigrant male performed
237 9 of these fights in order to gain access to the alpha female that was precociously receptive, hence,
238 reaching the alpha position on the 07/02/02. His tenure lasted until the 30/07/02 when a second
239 immigrant male challenged him in four fights and won the access to the only female that was
240 receptive this week.

241
242 Among the resident males, we found that the two PR males were the highest-ranking males,
243 which corroborates the predictions by Broom and colleagues (2004). In the general male hierarchy,
244 they were second and third higher-ranking males. Based on previous observations of the group we
245 assume that they were also among the three oldest males of the group. Furthermore, during the
246 previous mating season these two males were seen to form consortships and mate with the seven
247 mothers when they were receptive (Benetton et al. *in prep*).

248

249 **Aggression by females**

250 During our study, we observed 392 agonistic interactions of females towards other adult
251 members of the group. The following tests ($N = 4$) required a Bonferroni correction with $\alpha' =$
252 0.01250. Adult females attacked other adult females 283 times and adult males 109 times, a
253 difference that is not statistically significant when taking the number of females and males into
254 account (34 females, 12 males; two-tailed Chi-square test $\chi^2 = 0.318$, $p = 0.5730$, $df = 1$). The 28
255 females without infants directed attacks significantly more often at adult females than at adult
256 males (225 attacks against females and 25 against males; two-tailed Chi-square test $\chi^2 = 21.680$, $p <$
257 0.0001, $df = 1$). However, 5 of the 25 attacks against adult males were in support of attacked
258 mothers. Furthermore, females without infants directed aggression less often against mothers than
259 against other adult females (23 attacks against mothers and 202 against females corrected for
260 number of mothers and non-mothers; two-tailed Chi-square test $\chi^2 = 9.180$, $p < 0.0023$, $df = 1$). The
261 seven mothers were significantly more aggressive against adult males than against adult females
262 (58 attacks against females and 84 against males; two-tailed Chi-square test $\chi^2 = 31.808$, $p <$
263 0.0001, $df = 1$). Almost all of the attacks of mothers directed against adult males (82 out of 84)
264 were counter-attacks in response to one of the 128 attacks by an immigrant male, i.e. the mothers
265 counter-attacked in 64% of cases (Fig. 4).

266 Each time immigrant male's attacks aimed unattended infant, mothers would roughly grab
267 their infant and turn around the male to try to bite him. In other cases, females would try to slap the
268 male or would even chase him along with the PR male.

269

270 **Proximity between males and females**

271 In order to test the hypothesis of bonding between mothers and putative fathers as a
272 counter-strategy for infanticidal risk, we analyzed the pattern of proximity between mothers and
273 adult males. The following tests ($N = 4$) were corrected by Bonferroni with $\alpha' = 0.01250$. Per 100
274 minutes of observation, mothers were close to resident males 72.35 minutes (ranging from 65 to 79

275 minutes) during the vulnerable period (VP) of their infants, and 33 minutes (ranging from 24 and
276 54 minutes) when their infants were more than six months old (not vulnerable period NVP). Hence,
277 mothers were significantly closer to the resident males during VP than during NVP (two-tailed
278 Mann-Whitney-U test: $U = 0.00$, $p = 0.0017$). In contrast, mothers were close to immigrant males
279 only 8 minutes (ranging from 5.35 and 12.5 minutes) during the vulnerable period of their infants,
280 and 33 minutes (ranging from 18 and 47 minutes) when their infants were more than six months
281 old, which shows that mothers were closer to immigrant males during NVP than during VP.

282 Hence, if mothers were recorded at a comparable distance to resident and immigrant males
283 when their infants were more than six months old (two-tailed Mann-Whitney-U test: $U = 15.5$, $p =$
284 0.2502) (Fig. 4A), they were significantly more often registered near resident males than near
285 immigrant males during VP (two-tailed Mann-Whitney-U test: $U = 49$, $p = 0.0017$) (Fig. 5).
286 Furthermore, PR males were observed to actively gather mothers and infants after attacks by
287 immigrant males.

288

289 DISCUSSION

290 **Infanticidal risks in mangabeys: aggression by-product or behavioural strategy under sexual** 291 **selection?**

292 In the by-product hypothesis, infanticide is not a selected behaviour. Infants are not injured
293 or killed intentionally but because they are the most vulnerable individuals of the group. Hence,
294 infants' killing could happen during any males' intense enough conflicts. In this case, infants would
295 have the same probability to be injured by resident or immigrant males and males would not target
296 mothers and infants more than any other member of the group. Rather, infants' injuries would
297 happen when males are fighting each other and mothers either interfere in the conflict or remain
298 close-by. Furthermore, as the killing behaviour is accidental, females would not develop any
299 particular behavioural counter-strategies to prevent it. Conversely, in the sexually selected

300 hypothesis, infanticide is a behavioural strategy and concerns males that did not mate with mothers
301 the previous year. More precisely, the model developed by Broom and colleagues (2004) predicts
302 the occurrence of infanticide in multi-male primate species, if (1) male attackers' costs are
303 negligible and/or if (2) their status in the group allows them to get almost exclusive access to the
304 receptive females. Under this hypothesis, only some males would benefit from infanticide and
305 would target mothers and infants more than other member of the group. Furthermore, as infanticide
306 would be a selected behaviour, females would develop some counter-strategies.

307 In our study group, males did not fight each other very often and conflicts always arose
308 when the access for a receptive female was at stake. These conflicts did not last over long periods
309 and mainly involved the two protagonist males. Indeed, we recorded only four coalitions and
310 neither mothers nor females without infants were seen to intervene. Furthermore, no juveniles or
311 infants were involved in these conflicts, either intentionally or accidentally. In contrast, and mainly
312 outside the mating season, some of the immigrant males seized every opportunity to attack
313 mother/infant pairs or unweaned and unattended infants without any provocation from the females
314 (*pers. obs.*). None of these males had been seen mating with any of the group's females the
315 previous year (Benetton et al. *in prep.*). These same males hardly ever targeted juveniles or females
316 without infants. Resident males, in contrast, were more likely to attack females without infants than
317 mothers of dependent infants. Hence, the pattern of conflicts performed by the males in our group
318 tends to validate the sexually selected hypothesis rather than the by-product one.

319 Resident males' frequent counter-attacks probably made the infanticidal costs particularly
320 high for immigrant male attackers. Beside the risks of getting injured, the intensive chases they had
321 to flee from were likely to be energetically costly. However, if the costs were not negligible, at
322 times, the menstrual cycles of up to four females were synchronised. It allowed up to four high-
323 ranking males to form consortships simultaneously. As predicted by the sexually selected
324 hypothesis, most of the immigrating male attackers rose in the male hierarchy quickly after they

325 entered the group. Two of them even reached the alpha position during the course of the study and
326 increased their chances of siring the females' next offspring, as male ranks and mounting success
327 tend to be correlated.

328 During our study, one infant died before reaching one month old. A few days before the
329 infant's death, the mother was seen with a large and infected wound on her leg. At the same time,
330 the infant held its head on a strange angle and showed a general weakening which started with an
331 abnormal lethargy (indifference to surrounding group members). As we did not witness how the
332 mother and her infant were injured, we cannot give any evidence that this was the consequence of a
333 direct attack by a male. However, the mother had been attacked regularly before her infant died (8
334 attacks in 12 days) but was rarely attacked thereafter (4 attacks in the remaining 179 days). She
335 displayed a large sexual swelling within a month after the loss of her infant while mothers with
336 surviving infants did not. During the mating period, she was also seen mating with the two
337 immigrant male attackers that reached the alpha position. In this respect immigrant males that rose
338 in the male hierarchy were able to gain sexual access to a receptive mother and our results are in
339 agreement with many other studies supporting the sexual selection-hypothesis of infanticide.

340

341 **Mothers' counter-strategies: counter-attacks and cooperation with potential fathers**

342 As expected with the sexually selected hypothesis, mothers developed strategies that
343 seemed to reduce infanticidal risks. First, they regularly counter-attacked immigrant male attackers
344 during the infant's vulnerable period despite a sexual dimorphism that largely favours males during
345 aggression. Indeed males are larger, heavier and have longer canines and mangabey females, as
346 many other primate females (Hrdy 1977, Palombit 1999), seem to fail to form effective coalitions
347 against males. We recorded only five occurrences during which some females helped mothers.
348 However, if these mutual supports were rare, they involved at least from two to six other females

349 and did not seem correlated to matrilineal affiliations. Counter-attacks by females can probably
350 only partially reduce the risk of infanticide.

351 Resident adult males, however, that mated with the female and therefore were potential
352 sires, can provide considerable support for a mother against a potential infanticidal male (Hrdy
353 1979). Resident males who had been observed mating with the females the previous year (Benetton
354 et al. *in prep.*), strongly supported both infant/mother pairs and stray infants, and were sometimes
355 seen to groom the aggressed mothers after they had been attacked by immigrant males (24.3% of
356 the cases). These protective males were among the oldest and the highest-ranking males of the
357 group. Furthermore, mothers were recorded in close proximity of at least one resident male during
358 the period of infant vulnerability, while they avoided immigrant males. Our findings therefore
359 corroborate the results of some other studies on infanticide (e.g. Palombit et al. 1997, Borries et al.
360 1999b, Palombit 1999, 2000, Janson 2000), the mother/resident male cooperation is therefore likely
361 to be the key to reducing infanticide risk in sooty mangabeys.

362

363 **Conclusions**

364 Infanticide in mangabeys really follows model's predictions step-by-step. Firstly, male
365 attackers were usually immigrant males. They had no history of mating with the mothers of
366 unweaned infant they targeted and they managed to reach a position in the male hierarchy that
367 allowed them to have privileged accesses to receptive females. Secondly, protective males were
368 resident and old males. The previous mating season, they were seen to mate with the mothers of
369 unweaned infants. Thirdly, after the birth of their infants and to reduce infanticidal risks, mothers
370 used behavioural counter-strategies such as staying in the close vicinity of protective males.
371 Eventually, it would be interesting to investigate whether mangabey females also developed
372 counter-strategies prior to the conception of the infants.

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374

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507 **Figure legends**

508 **Figure 1:** Number of attacks performed by immigrant and resident males towards females with and
509 without infants. Males of each category are ordered by rank. 1 represents the highest-ranking male
510 of the category.

511

512 **Figure 2:** Number of attacks performed by immigrant and resident males towards another male
513 (either immigrant or resident). Males of each category are ordered by rank. 1 represents the highest-
514 ranking male of the category.

515

516 **Figure 3:** Number of attacks performed by immigrant and resident males towards another male
517 (either immigrant or resident). In white is represented the proportion (86%) of attacks given in
518 support of aggressed mothers while in black is represented the proportion of attacks that were not
519 performed in support of aggressed mothers.

520

521 **Figure 4:** Number of attacks performed by immigrant and resident males towards mothers or
522 unattended infants. In white is represented the proportion (64%) of attacks countered by mothers
523 while in black is represented the proportion of attacks that were not countered by mothers.

524

525 **Figure 5:** Number of minutes per 100 minutes of observation during which mothers were observed
526 at close proximity (less than 5 meters) from resident and immigrant males. The first graph
527 represents the proximities during the six months after infants were born and were considered
528 particularly vulnerable to infanticide (VP). The second graph represents the proximities after
529 infants were more than six months old (NVP).

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Figure 1

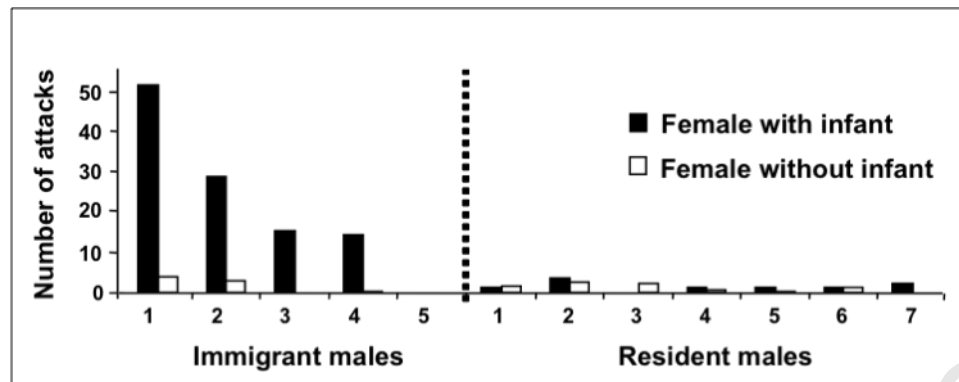
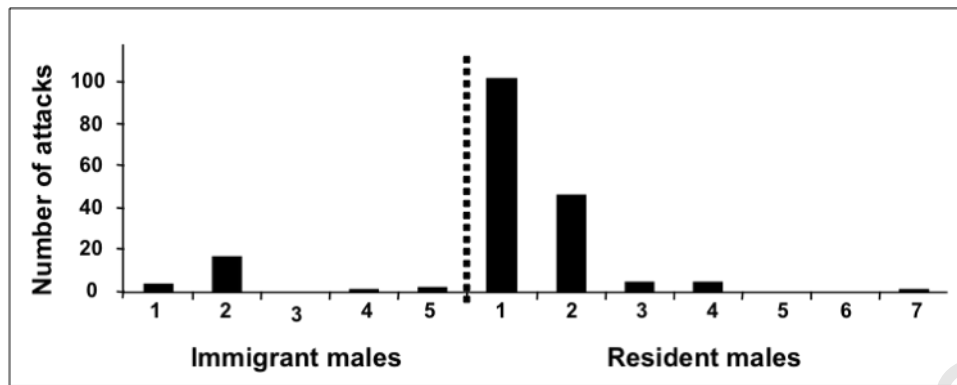
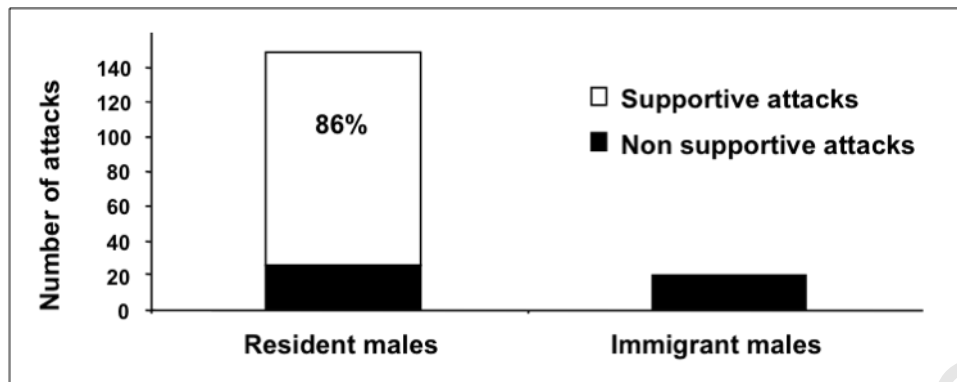


Figure 2



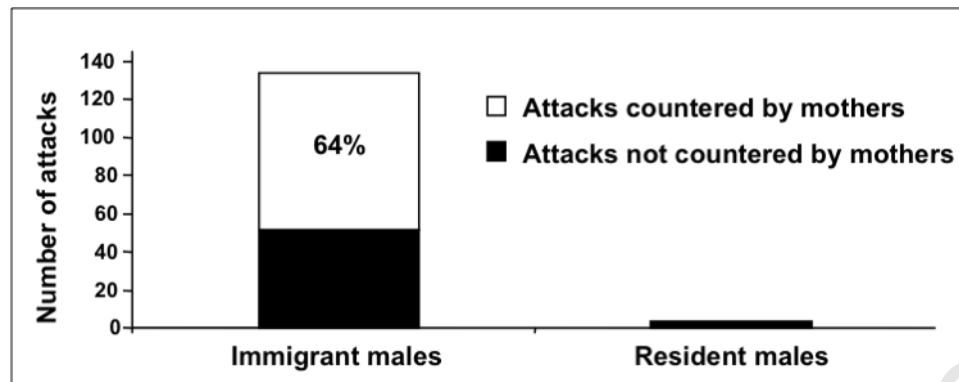
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Figure 3



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Figure 4



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Figure 5

